

JOURNAL

OF THE

New York Entomological Society

VOL. LIV

MARCH, 1946

No. 1

THE ELECTRORETINOGRAM AS A MEASURE OF WAVE-LENGTH SENSITIVITY TO LIGHT*

BY THEODORE LOUIS JAHN

ZOOLOGICAL LABORATORIES, STATE UNIVERSITY OF IOWA

The voltage developed across the retina of vertebrates when the eye is illuminated by light of different wave-lengths has been used by various investigators to determine the spectral sensitivity of the eye (Graham and Riggs, 1935; Graham, Kemp, and Riggs, 1935; Granit and Munsterhjelm, 1937; Granit and Wrede, 1937; Therman, 1938; earlier work reviewed by Kohlrausch, 1931, and Granit, 1936). The possibility of determining the spectral sensitivity of insects and other invertebrates in this manner has been pointed out by Crescitelli and Jahn (1939), Jahn and Crescitelli (1939), and Jahn (1940, 1942). Recently the work on the electrical response of the insect eye has been reviewed by Weiss (1944, 1945) who emphasized the similarity between the voltage-wave-length curves of the electroretinogram (ERG) and those obtained in behavior studies by Bertholf (1931, 1932) and by Weiss, Soraci, and McCoy (1941, 1942, 1943), Weiss (1943a) and Weiss, McCoy, and Boyd (1944). Inasmuch as consideration of the ERG as an index of visual sensitivity seems destined for considerable future attention, it is probably worthwhile to emphasize certain advantages of the method and also certain necessary precautions and to present a further analysis of the data of Crescitelli and Jahn (1939) on *Melanoplus*.

* Aided by a grant from the Rockefeller Foundation for research on the Physiology of the Normal Cell.

APR 22 '46

The studies of Crescitelli and Jahn were made primarily to determine whether or not there was a specific effect of wave-length of stimulating light on the wave-form of the ERG. It was proven conclusively that in *Melanoplus differentialis* and *Samia cecropia* that the wave-form is a function of intensity and that there is no effect of wave-length *per se*. This was an important point since the existence of such an effect would be evidence of the existence of true color vision. (The converse is not necessarily true.) The voltage-wave-length curves were not of primary interest at that time, and a complete analysis of them was not presented. However, the published data on *Melanoplus*, although incomplete in certain respects and intended for quite a different purpose, are valid as far as they go, and in view of the problem of wave-length sensitivity, they seem worthy of further consideration.

TREATMENT OF DATA

In several papers in which the ERG has been used in an attempt to determine the spectral sensitivity of the eye the voltage has been plotted against wave-length. The use of such curves has been criticized by Hecht and Pirenne (1940), who emphasized the necessity of plotting the reciprocal (or the log of the reciprocal) of the intensity necessary to produce *the same physiological response* (e.g., an ERG of given magnitude and wave-form) against wave-length. This point is well taken, and the recommended method is the only one which permits a comparison of the "sensitivity" curve with the absorption curve of the visual pigment (see also, Hecht, 1937). The reason for making this distinction is that in the use of voltage-wave-length curves it is assumed that the voltage-log *I* curve is linear, and this assumption is true only over a limited range (Hartline, 1928; Graham and Riggs, 1935; Wulff, 1943; and others). Graham and Riggs (1935) and Graham, Kemp, and Riggs (1935) plotted the reciprocal of the intensity necessary for a given electrical response against wave-length in their studies of the visibility curve of the white rat and the pigeon, and they obtained data which closely approximate the known visibility curves for other vertebrates.

A close similarity has been observed between voltage-wave-length and known or presumed visibility curves, but this close

similarity should be considered a coincidental rather than a necessary relationship. In animals in which neural elements may contribute to the ERG the voltage-wave-length curves merely give a rough approximation of the form of the sensitivity-wave-length curve. In fact, the only dependable characteristic of such curves is the position of the maxima or minima, and the ratio of the values of voltage at two wave-lengths bears no necessary relationship to the ratio of the sensitivity of the eye at these two wave-lengths. The approximation of the human visibility curve by the voltage-wave-length curve of the frog eye (Granit and Munsterhjelm, 1937; Granit and Wrede, 1937; Therman, 1938) is apparently without a necessary logical basis except for the position of the maximum. Hartline (1930) in his study of dark adaptation in *Limulus* obtained very similar curves for voltage-wave-length and for reciprocal intensity-wave-length. However, this relationship was not true for responses of small magnitude, and the similarity is not of general significance.

Apparently the usual reason why students of the ERG have not obtained $1/I$ -wave-length curves is that more numerous records are necessary for voltage-wave-length curves, and the physiological state of the eye is not easily controlled over the necessarily longer period of time. This, however, is not true of most of the insects which do not possess a diurnal rhythm, and *Melanoplus* seems to be a satisfactory animal for that purpose.

THE ERG OF MELANOPLUS

The data for the present analysis are taken from Figure 1 of the paper by Crescitelli and Jahn (1939). In this figure the ERG is given for various wave-lengths and intensities of the stimulating light. An attempt was made to match the wave-form and voltage of the ERG for various wave-lengths, and the intensity at which the match occurred is marked on each record. Therefore, the recorded intensities for each matched series gives us a measure of the relative intensity necessary to produce a given response. The figure contains seven series of ERGs, and six of these (rows 1 to 6) are well matched; the seventh is of dubious value for the present purpose.

These data are given in Figure 1. The reciprocal of the intensity measured in arbitrary units (the unit was the intensity

necessary to give the same thermopile-galvanometer deflection as 4 foot-candles of visible light from a 500-watt tungsten lamp)

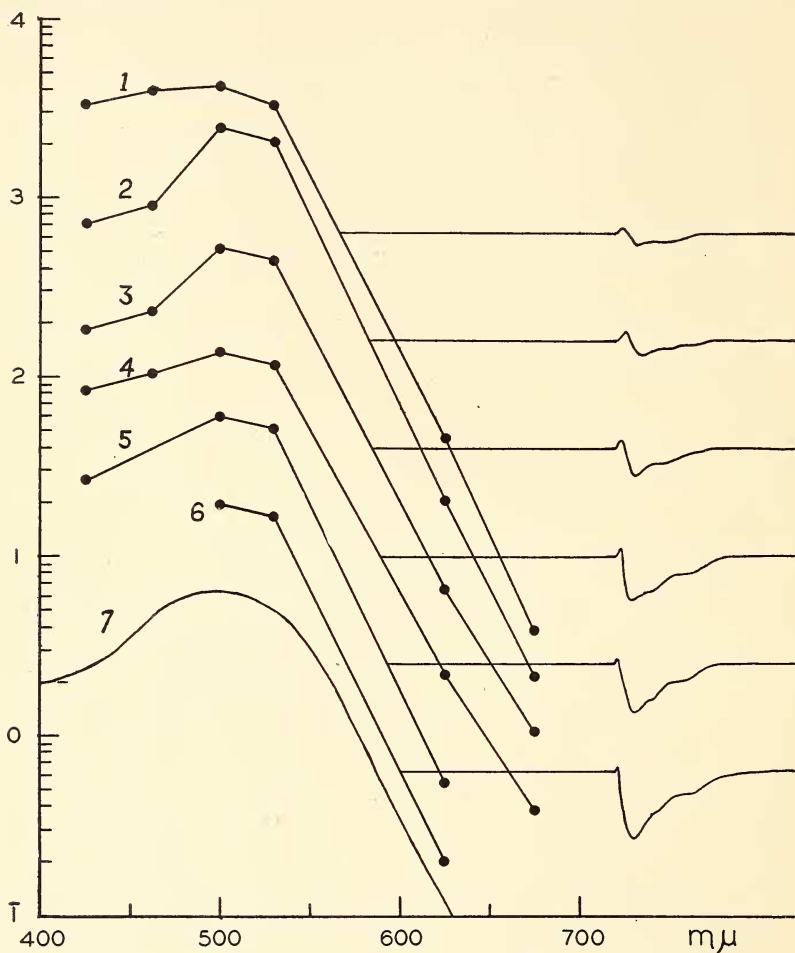


FIG. 1. Curves 1-6, the logarithm of the reciprocal of the intensity necessary to produce a given wave-form and magnitude of the ERG plotted against wave-length of stimulating light in millimicrons, *Melanoplus differentialis* data of Crescitelli and Jahn (1939). On the right is a copy of the ERG at each level of response. Curve 7, absorption curve of visual purple, logarithm of photometric density plotted against wave-length.

necessary to produce a given electrical response is plotted on a logarithmic scale against wave-length. The curves are numbered

in accordance with the rows in the original figure, and the waveform and relative magnitude of each response level are indicated by the corresponding diagrams of the ERG. The ordinate has been made logarithmic because of the wide range of values. In Figure 2 the same data have been plotted on an arithmetic scale

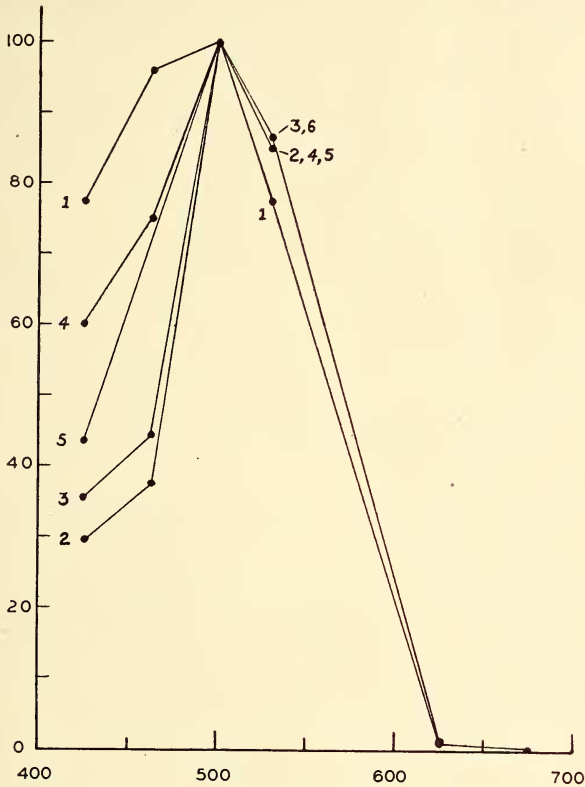


FIG. 2. Percentage effectiveness of light in producing a given ERG plotted against wave-length. Same data as Figure 1. Ordinate is per cent of the reciprocal of the intensity with the data for 500 millimicrons set at 100.

where the ordinate is the percentage of the reciprocal of the intensity centered at 500 mμ.

All data to the right of the peak are quite consistent; data to the left show a considerable variation. Curve 1 was obtained with very small responses which could not be matched as accurately as those for curves 2 to 5. Therefore, it is concluded that

curves 2 to 5 give the closest available approximation of the wave-length-sensitivity curves for *Melanoplus*.

DISCUSSION

These curves for *Melanoplus* are in general agreement with those obtained for the behavior of numerous insects by Weiss *et al.* (1941-1944) in that there is a peak at about 500 m μ , a great decrease on the longer wave-length side, and a lesser decrease on the short wave-length side. Other work on the spectral sensitivity of insects is reviewed by Weiss (1943). The similarity of the present curves for *Melanoplus* and the absorption curve for visual purple (review, Hecht, 1942) is more pronounced than of those given by Crescitelli and Jahn (1939).

The obvious advantage of the electrical method over that of behavior studies is that the sensitivity is determined independently of the reactions of the animal. Any definite discrepancy between the results of electrical and behavior methods when used on the same animal under comparable conditions would constitute positive evidence of wave-length discrimination, *i.e.*, of true color vision. At present, data suitable for such a comparison apparently do not exist.

Other electrical methods, which are applicable both to the problem of wave-length sensitivity and to that of wave-length discrimination, involve the study of single neural units. Graham and Hartline (1935) dissected the optic nerve of *Limulus* so that the response of single fibers to different wave-lengths of light could be recorded. Granit (Granit and Svaetichin, 1939; Granit, 1941, 1943, 1945, and others) placed micro-electrodes on single neurones in the retina of a variety of vertebrates. By these methods reciprocal energy-wave-length curves were obtained. Granit found that in some vertebrate retinae the peak sensitivity is quite different for different neural units. This is excellent proof not only of the existence but also of the mechanism of color vision. So far these methods have not been applied to insects.

The most recent treatment of color vision in insects is the report of extensive field experiments by Milne and Milne (1945).

LITERATURE CITED

- BERTHOLF, L. M. 1931. The distribution of stimulative efficiency in the ultraviolet spectrum for the honey bee. Jour. Agr. Res., 43: 703-713.

- . 1932. The extent of the spectrum for *Drosophila* and the distribution of stimulative efficiency in it. *Zeitschr. f. vergleich. Physiol.*, 18: 32-64.
- CRESCITELLI, F., AND T. L. JAHN. 1939. The electrical response of the dark-adapted grasshopper eye to various intensities of illumination and to different qualities of light. *Jour. Cell. and Comp. Physiol.*, 13: 105-112.
- GRAHAM, C. H., AND H. K. HARTLINE. 1935. The response of single visual sense cells to lights of different wavelengths. *Jour. Gen. Physiol.*, 18: 917-931.
- , E. H. KEMP, AND L. A. RIGGS. 1935. An analysis of the electrical retinal responses of a color discriminating eye to lights of different wavelengths. *Jour. Gen. Psychol.*, 13: 275-294.
- , AND L. R. RIGGS. 1935. The visibility curve of the white rat as determined by the electrical retinal response to lights of different wavelengths. *Jour. Gen. Psychol.*, 12: 279-294.
- GRANIT, RAGNAR. 1936. Die Elektrophysiologie der Netzhaut und des Sehnerven. *Acta Ophthal. Supp.*, 8, 14: 1.
- . 1941. The retinal mechanism of color reception. *Jour. Opt. Soc. Am.*, 31: 570-580.
- . 1943. A physiological theory of color perception. *Nature*, 151: 11-14.
- . 1945. The color receptors of the mammalian retina. *Jour. Neurol.*, 8: 195-210.
- , AND A. MUNSTERHELM. 1937. The electrical responses of dark adapted frog's eyes to monochromatic stimuli. *Jour. Physiol.*, 88: 436-458.
- , AND G. SVAETICHIN. 1939. Principles and technique of the electrophysiological analysis of color reception with the aid of microelectrodes. *Uppsala Lak-Foren. forb., N.F.*, 45: 161-177.
- , AND C. M. WREDE. 1937. The electrical responses of light adapted frog's eyes to monochromatic stimuli. *Jour. Physiol.*, 89: 239-256.
- HARTLINE, H. K. 1928. A quantitative and descriptive study of the electric response to illumination of the arthropod eye. *Am. Jour. Physiol.*, 83: 466-483.
- . 1930. The dark adaptation of the eye of *Limulus*, as manifested by its electric response to illumination. *Jour. Gen. Physiol.*, 13: 379-389.
- HECHT, S. 1937. Rods, cones and the chemical basis of vision. *Physiol. Rev.*, 17: 239-290.
- . 1942. The chemistry of visual substances. *Ann. Rev. Biochem.*, 9: 465-496.
- , AND M. H. PIRENNE. 1940. The sensibility of the nocturnal long-eared owl in the spectrum. *Jour. Gen. Physiol.*, 23: 709-718.
- JAHN, T. L. 1940. Bioelectrical potentials as indices of physiological activity. *Gamma Alpha Record*, 30: 38-41.

- . 1942. The measurement of visual phenomena by means of the electroretinogram. *Proc. Iowa Acad. Sci.*, 49: 533-534.
- , AND F. CRESCITELLI. 1939. The electrical responses of the *Cecropia* moth eye. *Jour. Cell. and Comp. Physiol.*, 13: 113-119.
- KOHLRAUSCH, A. 1931. Elektrische Erscheinungen am Auge. *Handbuch der norm u. path. Physiol.*, 12/2, 2: 1393.
- MILNE, L. J., AND M. J. MILNE. 1945. Selection of colored lights by night-flying insects. *Ent. Americana*, 24: 21-86.
- THERMAN, P. O. 1938. The neurophysiology of the retina. *Acta Societatis Scientiarum Fennicae, Nova Series B*, 11: 1-74.
- WEISS, H. B. 1943. Color perception in insects. *Jour. Econ. Ent.*, 36: 1-17.
- . 1943a. The group behavior of 14,000 insects to colors. *Ent. News*, 54: 152-156.
- . 1944. Insect responses to colors. *JOUR. N. Y. ENT. SOC.*, 52: 267-271.
- . 1945. Insect response to colors. *Sci. Monthly*, 61: 51-56.
- , E. E. MCCOY, JR., AND W. M. BOYD. 1944. Group motor responses of adult and larval forms of insects to different wave-lengths of light. *JOUR. N. Y. ENT. SOC.*, 52: 27-43.
- , E. A. SORACI, AND E. E. MCCOY, JR. 1941. Insect behavior to various wave-lengths of light. *JOUR. N. Y. ENT. SOC.*, 49: 1-20; 149-159.
- . 1942. Insect behavior to various wave-lengths of light. *JOUR. N. Y. ENT. SOC.*, 50: 1-35.
- . 1943. Insect behavior to various wave-lengths of light. *JOUR. N. Y. ENT. SOC.*, 51: 117-131.
- WULFF, V. J. 1943. Correlation of photochemical events with the action potential of the retina. *Jour. Cell. and Comp. Physiol.*, 21: 319-326.